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PRELIMINARY INVESTIGATIONS OF HYMENAEA COURBARIL AS A RESIN PRODUCER

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DATA HAVE RECENTLY BEEN PRESENTED to suggest that Oligo-Miocene amber from Chiapas, Mexico, was produced by an ancestral population of the leguminous genus *Hymenaea* (Langenheim, 1963; Langenheim & Beck, 1965; Langenheim, 1966). Evidence for this source was obtained through comparison of infrared spectra of the amber and resin from living populations of *Hymenaea courbaril* L., and supported by the presence of *Hymenaea* leaflets in the amber. The evidence was further corroborated by the discovery that the amber had been deposited at or near mangrove vegetation, a habitat in which *H. courbaril* occurs commonly today (Langenheim, Hackner, & Bartlett, 1967). This determination of a leguminous source is in contrast to the classic concept of amber as generally derived from pines or at least from conifers.

The usual preconception of pine origin of amber results from relatively detailed studies of the extensive early Tertiary amber deposits along the Baltic coast (Conwentz, 1890; Schubert, 1953, 1961; Langenheim, 1964). Inclusions in the Baltic amber of needles and staminate cones of pines usually have been cited as a basis for origin, although other coniferous remains, as well as certain angiospermous ones, are more abundant than those of pines. The most convincing evidence for pine origin is droplets of amber found in resin canals in the xylem and around parenchymatous cells of the inner living bark (Schubert, 1953, 1961). Several species of pines were thought to have been involved in production of the Baltic amber but these are now all treated as a single species, *Pinus succinifera* (Conw.) Schubert.

The great quantities of amber found in these Baltic deposits, sufficiently extensive to have been mined for centuries on the Samland Peninsula, opened questions as to how so much resin was produced. Because pines commonly do not exude this quantity of resin "naturally," it was assumed that a pathological condition known as "succinosis" must have existed (Conwentz, 1890). Not only did Conwentz and his followers think that pathological conditions were necessary, but that the entire forest must have been diseased to have produced such deposits of amber, "Es gab kaum einen gesunden Baum im ganzen Bernsteinwald — das Pathologische war die Regel, das Normale die Ausnahme!" Czeczott (1960) has pointed out that this picture of the "sick amber forest" was so masterfully presented by Conwentz that his view has "hypnotized" workers for almost 60 years. Schubert (1953, 1958, 1961) thought that the abnormally intensified resin production might have been caused by a "strong disturbance of physiological balance," some of which might possibly have resulted from trees being exceptionally susceptible to injury near the periphery of their distribution. Only a few investigators such as Klebs (Kunz, 1903) and Bachofen-Echt (1930, 1949) have indicated that the Baltic amber accumulations could have resulted from normal production of resin. They thought that pines, dominant in forests over extensive areas for millions of years, could account for the large quantities of amber found in the Baltic deposits.

Although the flora occurring in the Baltic amber has been known to contain a large tropical element, except for Schubert's (1958) reference to warm temperate pines, no one seems to have recognized that trees produce more copious amounts of resin in tropical environments than in temperate ones. Likewise it has not been pointed out that angiosperms belonging to such families as Leguminosae, Burseraceae, Guttiferae, Anacardiaceae and Dipterocarpaceae can produce as much or more resin than gymnosperms. Moreover, many of these angiosperms seem to produce large quantities of resin under natural forest conditions. At least resin accumulates in the soil today in sufficient amounts to justify collection for commercial purposes. Thus the Chiapas amber project has directed our attention to a tropical angiosperm which has produced sufficiently large quantities of resin in an environment where it could become incorporated into the geologic record. The Chiapas amber likewise has an advantage in being chemically stable enough to allow comparison with resin from living populations. The opportunity to compare the fossil and modern resins has brought up various questions, such as what genetic and environmental conditions control chemical composition as well as yield of resin. What are the conditions in tropical environments that result in active biosynthesis as well as exudation of resin to the surface of the plant where large quantities may accumulate? In what tissues does biosynthesis occur and what are the variations in production during the ontogeny of the plant? To answer these questions, resin production in populations of *Hymenaea courbaril* is being studied ecologically in the field and morphogenetically in the laboratory. This paper constitutes a preliminary report on field studies and initial morphogenetic considerations of a planned long-range investigation.

TAXONOMIC AND ECOLOGIC PERSPECTIVE

The genus *Hymenaea*, subfamily Caesalpinioideae, family Leguminosae, has the center of its distribution in the Brazilian Amazonian region (Record & Hess, 1943). East African and Asiatic species of *Trachylobium* resemble *Hymenaea* and sometimes have been included in the genus, as have some South American species of *Peltogyne*. Twenty-seven species are commonly recognized; the number can be greater if several varieties of *H. courbaril* are considered worthy of specific recognition. Twelve species (*H. davisii* Sandwith, *H. microcarpa* Huber, *H. palustris* Ducke, *H. oblongifolia* Huber, *H. parvifolia* Huber, *H. pororoca* Huber, *H. velutina* Ducke, *H. reticulata* Ducke, *H. intermedia* Ducke, *H. floribunda* HBK., *H. venosa* Vahl, *H. rubriflora* Ducke) have their distribution centered in northern South America. They generally occur in the Amazonian region and adjacent areas in northern Brazil, Peru, Colombia, Venezuela, and the Guianas. Five species (*H. stigonocarpa* Mart., *H. stilbocarpa* Hayne, *H. martiana* Hayne, *H. splendida* Vogel and *H. eriogyne* Benth.) generally occur in southeastern Brazil (from Bahia to Rio Grande do Sul) as well as in adjacent Paraguay and Bolivia. Six species (*H. adenotricha* Ducke, *H. multiflora* Kleinh., *H. sellowiana* Hayne, *H. chapadensis* Barb.-Rodr., *H. correana* Barb.-Rodr., *H. olfersiana* Hayne) are recorded only locally.

Hymenaea courbaril L. has a wide range of distribution, occurring in all of the South American countries except Argentina, Uruguay and Chile, on most of the islands of the West Indies, and along the Pacific drainage throughout Central America to central Mexico. Although this species generally appears to be distinctive from the other described species, confusion apparently does exist in distinguishing it from *H. oblongifolia* which occurs in the Amazonian area. *H. altissima* Ducke is often recognized as a variety of *H. courbaril* in southeastern Brazil. *Hymenaea candolliana* HBK. in Central America is so close morphologically that it frequently is considered either synonymous with or a variety of *H. courbaril*. Ducke (1949) indicates that the typical form of *H. courbaril* occurs in Colombia, Venezuela, the Guianas, the Antilles, and Central America as well as in the lower Amazonian area to the tributary Rio Tapanjós. However, he described the variety *subsessilis* from the region of Manaus and the variety *obtusifolia* from northeastern Brazil, particularly in Ceará and Bahia.

Hymenaea courbaril is commonly called Locust or Algarroba in the West Indies, Guapinol in Central America, and Jutahy or Jatobá in Brazil. This is the species of *Hymenaea* that produces the largest quantity of resin; therefore, it is the one from which resin has been collected for commercial usage. Other species of *Hymenaea* reported to yield resin in varying amounts are *H. intermedia, H. parvifolia, H. velutina*, and *H. stigonocarpa* (Tschirch & Stock, 1936). Detailed statements regarding resin production for the other species are not known to the author.

Hymenaea courbaril can reach a large size, i.e., 100 to 180 feet high, with a spreading crown supported by a large trunk sometimes more than six feet in diameter. The trees are taprooted when young but later develop a considerable ramifying root system. The tree reproduces extensively from root suckers and thus persists following cutting. In secondary vegetation in Central America it commonly attains only 40 to 60 feet in height and a diameter of 2 to 3 feet. Rarely today can one see the few remaining relatively undisturbed areas where these trees attain the large sizes reported by Freise (1934), Record and Hess (1943), et al.

This species, *Hymenaea courbaril*, seems to occupy a relatively wide range of habitats throughout its extensive distributional pattern. In Mexico and Central America it occurs in moist evergreen forests as well as seasonally dry ones (Miranda 1952–53; Miranda & Hernandez-X., 1963; Gómez-Pompa, 1965; Langenheim, 1966). The moist evergreen forest in Mexico (Selva Alta Perennifolia *sensu* Miranda) occurs where the median annual temperature is greater than 20° C., the annual precipitation greater than 1500 mm., and where there is a short dry period. Where precipitation is greater than 2000 mm., the dry period can be longer. Variations in this type of forest are numerous and characterized by some of the components tending to dominate in certain zones. *Hymenaea courbaril* occurs only sporadically in this forest type except in flooded areas or where soil moisture is abundant. For example, it grows amid such populations as *Ficus* spp. and *Andira* spp. which occur along banks or lowlands with rapid movement of water during flooding, with *Tabebuia pentaphylla* (L.) Hemsl. in lowlands with little movement of water during flooding, and with *Pachira aquatica* Aubl. on banks of muddy rivers which are flooded frequently. Some of these same riparian species also occur in the semideciduous types of forest (Selva Alta or Mediana Subcaducifolia *sensu* Miranda & Hernandez-X., 1963). These forests are characterized as ones in which 50 to 75 per cent of the trees lose their leaves during the peak of the dry season. The climate, like that of the Selva Alta Perennifolia, is characterized by a median annual temperature greater than 20° C. The annual precipitation is above 1200 mm., but there is an accentuated dry season. On the Pacific slopes in Mexico *H. courbaril* is one of the most characteristic trees in this forest type. Other populations occurring frequently with it are *Enterolobium cyclocarpum* (Jacq.) Griseb., *Cedrela mexicana* Roem., *Licania arborea* Seem., *Cybistax donnell-smithii* Rose, and *Hura polyandra* Baill. (Miranda & Hernandez-X., 1963). Actually "selvas de guapinol" occur along rivers or arroyos where soil is deep in southern Mexico (Miranda, 1952–53). Commonly occurring with *H. courbaril* are *Andira inermis* (Sw.) HBK., *Nectandra* spp., *Ficus glabrata* HBK., *Calophyllum brasiliense* Camb., *Brosimum costaricanum* Liebm. and *Tabebuia pentaphylla*. Among smaller trees (6–15 m.) the following are most frequent: *Trichilia cuneata* Radlk., *T. hirta* L., *Coccoloba cozumelensis* Hemsl., *Annona reticulata* L., *Swietenia humilis* Zucc., *Bursera simaruba* (L.) Sarg., *Psidium sartorianum* (Berg.) Nied., *Inga laurina* (Sw.) Willd., *Styrax argenteus* Presl, *Genipa americana* L. and *Karwinskia calderoni* Standl.

Hymenaea courbaril often occurs in Sabanas, i.e., grassy areas with scattered trees, in either the Selva Subcaducifolia or Selva Baja Subperennifolia. Here the soil is usually characterized by deficient drainage, i.e., muddy in the rainy season and parched in the dry season. *Licania* *arborea* and *Bursera simaruba* are common associates of *Hymenaea* in these habitats.

In certain stands of Selva Mediana Subcaducifolia *Hymenaea courbaril* can be sufficiently dominant to form essentially a consociation. It occurs in this manner along the Guerrero coast in Mexico on sandy soils derived from granitic parent materials. It likewise can appear in coastal sites on sandy plains or beach ridges intermingling with Selva Baja Caducifolia, i.e., with *Bursera* spp., *Pistacia mexicana* HBK., *Ceiba* sp., *et al.* In coastal areas such as these in Mexico, *H. courbaril* commonly comes in contact with mangrove swamps (Manglares). *Hymenaea* apparently grew near mangrove swamps during the Oligo-Miocene also in the Chiapas, Mexico, area, as evidence from a palynological study indicates that the Chiapas amber was deposited in or adjacent to mangrove vegetation (Langenheim, Hackner & Bartlett, 1967).

In Costa Rica *H. courbaril* also occurs in moist to relatively dry forest types. In the province of Guanacaste, it is an important element in the forest classified as Tropical Dry (Holdridge, 1964). The dry sites in Costa Rica, however, are considerably more mesic than those in Mexico. It generally grows on fertile, well-drained soils and is frequent along rivers with such associates as *Anacardium excelsum* (Bert. & Balb.) Skeels, *Enterolobium cyclocarpum*, *Cedrela mexicana*, *Tabebuia chrysantha* (Jacq.) Nichols., and *Achras* sp.

Hymenaea courbaril is a common component of the Subtropical or Premontane Moist forests (*sensu* Holdridge) in Costa Rica. Plots were made in this forest type near Villa Colón in the province of San José at approximately 900 m. altitude. Here the median temperature is above 20° C; the precipitation is about 2000 mm. annually, but there is a pronounced dry season from mid-November through April. The forest studied was near a river where the vegetation has been disturbed by long human occupation. The dominant trees are *H. courbaril*, *Brosimum* sp., *Tabebuia pentaphylla, Luehea candida* (DC.) Mart. and *Cupania guatemalensis* Radlk. (Fournier, personal communication).

On the Osa Peninsula of Costa Rica, *H. courbaril* occurs in a dense mixed forest (Tropical Wet *sensu* Holdridge or Lower Montane Rain Forest *sensu* Allen) where it reaches a height of over 120 feet and with a buttressed base 4 to 6 feet in diameter. Here it grows with *Virola* spp., *Vantanea* sp., *Vochysia* spp., *Carapa* sp., *Calophyllum brasiliense*, and *Copaifera trapezifolia* Hayne. This forest type develops where the median annual temperature is greater than 24° C and annual precipitation is greater than 4000 mm.

It is reported that *Hymenaea courbaril* occurs in both moist and dry coastal forests in Puerto Rico, as well as on other islands of the West Indies (Little & Wadsworth, 1964).

Despite the abundance and economic importance of *H. courbaril* in Brazil, little ecologic information seems available. Freise (1934) does state that in Brazil it occurs in a variety of habitats, from sterile, sandy soils along the coast to well-drained soils in the midst of Amazonian forests. In the Amazonian region difference in size of the trees apparently can be correlated with edaphic conditions (Rodrigues, personal communication). The trees attain a greater diameter, although not necessarily greater height, on fertile floodplain soils than on relatively more sterile upland soils.

One would expect *Hymenaea courbaril* to be differentiated into ecological races, since it has occupied different climatic and edaphic conditions over a wide distributional range probably for long periods of time. Morphological differences have been recognized by description of varieties, but no evaluation of the variation pattern has been attempted, as is true for most genera from this part of the world. Nor are data available regarding genetic and physiological differences which might provide illumination concerning both chemical composition and yield of resin.

Even though *H. courbaril* probably is ecotypically differentiated, what effect this might have on resin composition is not definitely known. Investigations present varying results for species populations within different genera. Baker and Smith (1901, 1920) in pioneer studies of the chemical composition of *Eucalyptus* oils found that generally, except for perhaps half a dozen, all species possess comparatively constant chemical characteristics throughout their geographical distribution. Penfold and Morrison (1927), however, discovered some forms of *Eucalyptus dives* Schauer in which the essential oils varied in composition, and they concluded that these variations were due to genetic rather than environmental differences. In a later study, Penfold and co-workers (1948) also showed differences in the composition of the oils in physiological races of *Leptospermum citratrum* Shallinor.

Krestinsky et al. (1952), found that turpentine of *Pinus sylvestris* L. from different ecological sites in forests possessed the same physical properties and chemical composition. Mirov (1948), however, indicates that *P. sylvestris* has several physiological races and questions whether or not Krestinsky dealt with only one of these. Mirov further points out that when the physical characters (reflecting the chemical composition) of turpentine of the genus *Pinus* are studied, some species vary but little throughout their range, whereas others vary a great deal. *Pinus merkusii* De Vries, which grows over a wide range in Burma and Indonesia, varies but little in the physical characters of its turpentine. On the contrary, the chemical composition of the turpentine of *Pinus ponderosa* Laws. (Mirov, 1958, 1961) varies with the several physiological races which have been identified. Mirov also noted that variation in chemical composition of the turpentine may be a result of hybridization in some cases.

CHEMICAL COMPOSITION OF THE RESIN

The pale yellow to reddish resin (sometimes referred to as a resin-like gum) produced by *Hymenaea* has been known in the commercial trade as "South American Copal" to distinguish it from various copals from other parts of the tropics (Tschirch & Stock, 1936). As a result of the varied usage in literature two semantic confusions need to be clarified. First is the distinction between gums and resins. These products are synthesized through different metabolic pathways. Chemically gums are hydrophilic polysaccharides. Resins (often called oleoresins or balsams) are complex mixtures of mono-, sesqui-, and di- and triterpenoids. These terpenoids are built on a fundamental isoprenoid pattern regarded as evolutionary modifications of a primeval mevalonic acid pathway (Robinson, 1963). Gums are readily distinguished from resins by their ability to dissolve in water or to absorb water to form a jelly or gelatinous paste, and by their inability to dissolve in hydrocarbons which are solvents for resins. Although a small polysaccharide fraction is present in the product from *Hymenaea*, this material primarily is composed of terpenoid constituents. In order to indicate this polysaccharide component, the product from *Hymenaea* justifiably can be called a gum-resin, but not a gum *per se*. Part of the confusion with the term "gum" results from lax usage in the commercial literature, but it also may be due to the tendency of some botanists to refer to resinous secretions from angiosperms as "gums."

Confusion also exists with the term "copal," as it is used to connote resins from different plant families. The word probably has a Mexican origin, being derived from "copalli," meaning incense. In Mexico, however, the natives do not use "copal" or "copalli," to refer to resins from members of the Leguminosae but rather to those from the Burseraceae. In the commercial resin literature, nonetheless, "copal" certainly is more commonly used for resins of various leguminous genera, particularly the African *Trachylobium*, *Copaifera* (including *Guibourtia*), *Daniellia* et al., as well as *Hymenaea* in Central and South America. Copal also is used for resin from the gymnospermous *Agathis alba* (Lamb.) Foxw. in the East Indies and Philippines.

Throughout the wide distributional range of *H. courbaril*, natives use the resin for incense and generally as a cement. Extensive commercial usage, however, seems to have developed primarily in Brazil. Here it has been employed chiefly in the manufacture of special grades of varnish and to a limited extent for medicinal purposes. Howes (1949) reports that Brazilian copal is recovered frequently from water courses and varies in size from a pea to that of a man's fist. When dug from the ground, it may be in large, irregularly shaped pieces. Record and Hess (1943) indicate that "the gum gatherers dig around the roots and sometimes obtain a barrelful of copal lumps in a place, while the former site on a big tree, long since decayed, may yield several barrels of so-called fossil copal." Although resin apparently has been collected from various areas in Brazil, the great collection center seems to have been in the Amazonian region — the Ilha do Marajó near Belém and along Amazonian tributaries such as the Tapanjós and Xingu. *Hymenaea* resin also was collected and used by pre-Columbian aborigines in southern Costa Rica and Panama (Balser, 1960). Noriega (1918) likewise reports the economic value of *Hymenaea* resin in Oaxaca, Mexico, where large masses again are found in the soil.

Early chemical analyses of *Hymenaea* resin have been made in this commercial context. Freise (1934) analyzed resin from *H. stilbocarpa* in three conditions: 1) freshly flowing, 2) fresh resin from a recent cut in bark, 3) buried in the soil. The terms "fossil" and "subfossil" are used frequently in the commercial literature to refer to resins buried in the soil. This is a different connotation from that generally employed by geologists in which prehistoric conditions are at least implied. At our present state of knowledge, the processes involved in fossilization of resin appear to be progressive oxidation and polymerization. At what point a resin actually is considered to be fossilized has not yet been defined. Freise discovered that between the free-flowing and the buried states, the resin becomes harder, darker in color, and considerably more insoluble in alcohol. The melting point range increases from 180 to 192° C. for fresh resin from a bark wound to 265° C. plus, for an old, buried resin. The resin acid content varies from 8 to 16 per cent in the fresh, flowing resin, 32 to 38 per cent from the wound in the bark, 50 to 55 per cent in young, buried resin to 55 to 68 per cent in the old, buried resin. This increase in resin acid content may be due to volatilization of components initially present. Nakano and Djerassi (1961) have made the only modern analyses known to the author on the resin acid constituents of *H. courbaril*. They investigated a single sample from Brazil and did not indicate whether or not it came from the tree or was buried in the ground. They reported that the acidic fractions of this sample consist largely of a diterpene acid which they named copalic acid. Copalic acid has the same carbon skeleton of agathanedicarboxylic acid and related diterpene acids (cativic, eperuic and labdanolic) and appears to correspond in absolute configuration to dehydroeperuic acid. These latter resin acids occur in *Prioria copaifera* Griseb., *Eperua falcata* Aubl., and *Cistus ladanum* [1] Le Maout & Dcne.

Corroborative evidence that an ancestral population of *Hymenaea courbaril* is the source of Oligo-Miocene amber from Chiapas, Mexico, was provided by comparing infrared spectra of the amber with spectra of resin from trees living today (Langenheim & Beck, 1965; Langenheim, 1966). Infrared spectrophotometry offers a simpler means of relating chemical composition to the botanical origin of amber than other techniques now recorded. Because amber is so highly polymerized, only small percentages of the material are readily soluble. The infrared technique provides a means whereby the whole amber can be analyzed in the solid state by dispersing it in potassium bromide pellets. Also the large number of absorption bands that amber and modern resin show offer a multiplicity of parameters from a single experiment.

In the study of the Chiapas amber, spectra were made from living trees whose ancestors might have produced the amber, such as: *Styrax, Amyris, Myroxylon, Guaiacum, Pistacia, Bursera, Hymenaea, Protium, Pinus, Taxodium*, etc. The spectrum for each genus was clearly distinguishable

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[1] This name, supplied by a colleague in chemistry, was used by LeMaout and Decaisne in the legend to an illustration and is cited in Index Londinensis. It is probable that the name *Cistus ladaniferus* L. was intended.

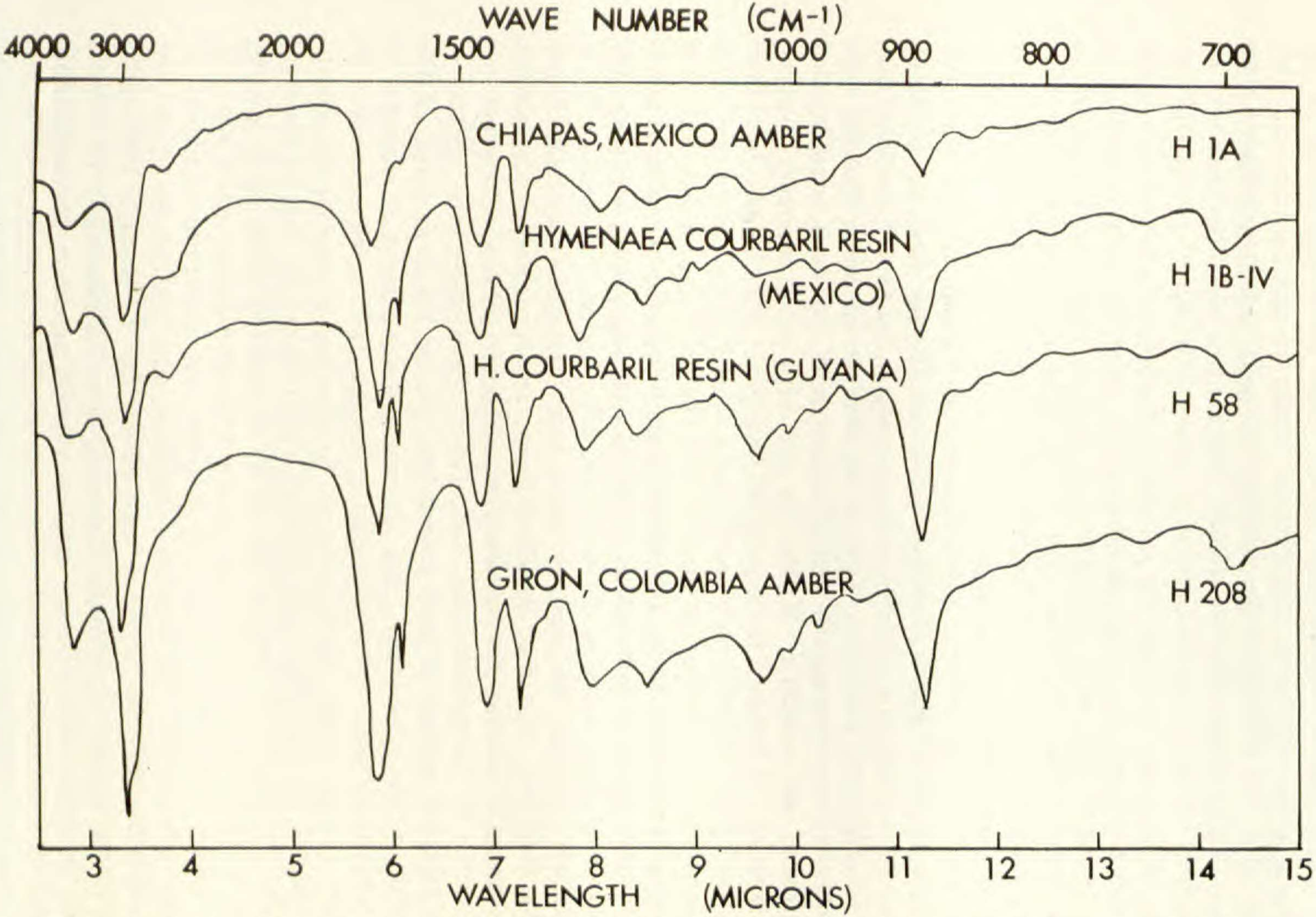

FIG. 1. Infrared spectra of Oligo-Miocene amber from Chiapas, Mexico, and resin from extant *Hymenaea courbaril* from Mexico; amber from Girón, Colombia, and resin from extant *Hymenaea courbaril* from Guyana.

(Langenheim & Beck, 1965; Langenheim, 1966). Populations of certain species, as well as closely related species within a genus, were found to have characteristic, reproducible spectra. Also all of the spectra of the Chiapas amber specimens analyzed are similar to spectra from *H. courbaril* (FIG. 1), although some samples are more closely correlated than others. Langenheim and Beck (1965) indicate that the differences may be explained by the progressive effects of both oxidation and polymerization.

In order to try to assess the variability in chemical composition of the hardened present-day resin, as expressed in infrared spectra, samples of *H. courbaril* resin were obtained from various localities throughout its wide distribution. Problems exist in obtaining resin samples that have adequate information substantiating their determination. Samples and voucher specimens were collected in the field in Mexico, Costa Rica, and Brazil by the author. Specimens were also obtained from resin collections of the Chicago Museum of Natural History and the Botanical Museum of Harvard University, from Guatemala, Guyana, Venezuela, Brazil, Ecuador, and Dominica. There is no absolute assurance that the resin specimens from the museums were produced by *H. courbaril*, as no voucher collections are available. Within the risk of a possible error, however, these resins are assumed to be properly identified. Samples also have been analyzed from different trees in the same local populations in the states of Guerrero and Chiapas in Mexico, and the provinces of San José and Puntarenas in Costa Rica. Likewise spectra of samples of oxidized resins have been run from different parts of the tree, i.e., trunk, branches, and roots, in addition to pieces buried in the soil. FIGURE 2 presents a representative spectrum for samples taken from Mexico, Guatemala, Costa Rica, Dominica, Ecuador, Brazil, Guyana, and Venezuela. The spectra are generally similar to one another, although certain differences are apparent. As Langenheim and Beck (1965) have stated, the identity of two infrared spectra of pure compounds can be taken as proof of the identity of the compounds. But for resins, which consist of mixtures of components of high average molecular weight, two restrictions must be made: 1) only major constituents can be expected to give strong absorption bands, so that differences in minor constituents may not be apparent at all; 2) identity of spectra can never be expected even from samples from a single specimen, but the presence of similarities, particularly in the upper "fingerprint" region is evidence for structural similarity of major constituents. The variations displayed may possibly be a reflection of a slightly different chemical composition due to ecotypic differentiation of the various populations. Certainly from the indications of Mirov's work, ecotypic differentiation and consequent variation in composition might be expected in a species with such a wide distributional range and occurrence in different environmental conditions. Fresh resin, however, might reflect ecotypic variation better than the resin changed by oxidation and polymerization. In pines, the mono- and sesquiterpene fractions (turpentine) are useful, in some cases, in indicating racial differences (Mirov, 1961), whereas a large portion of the remaining resin fraction

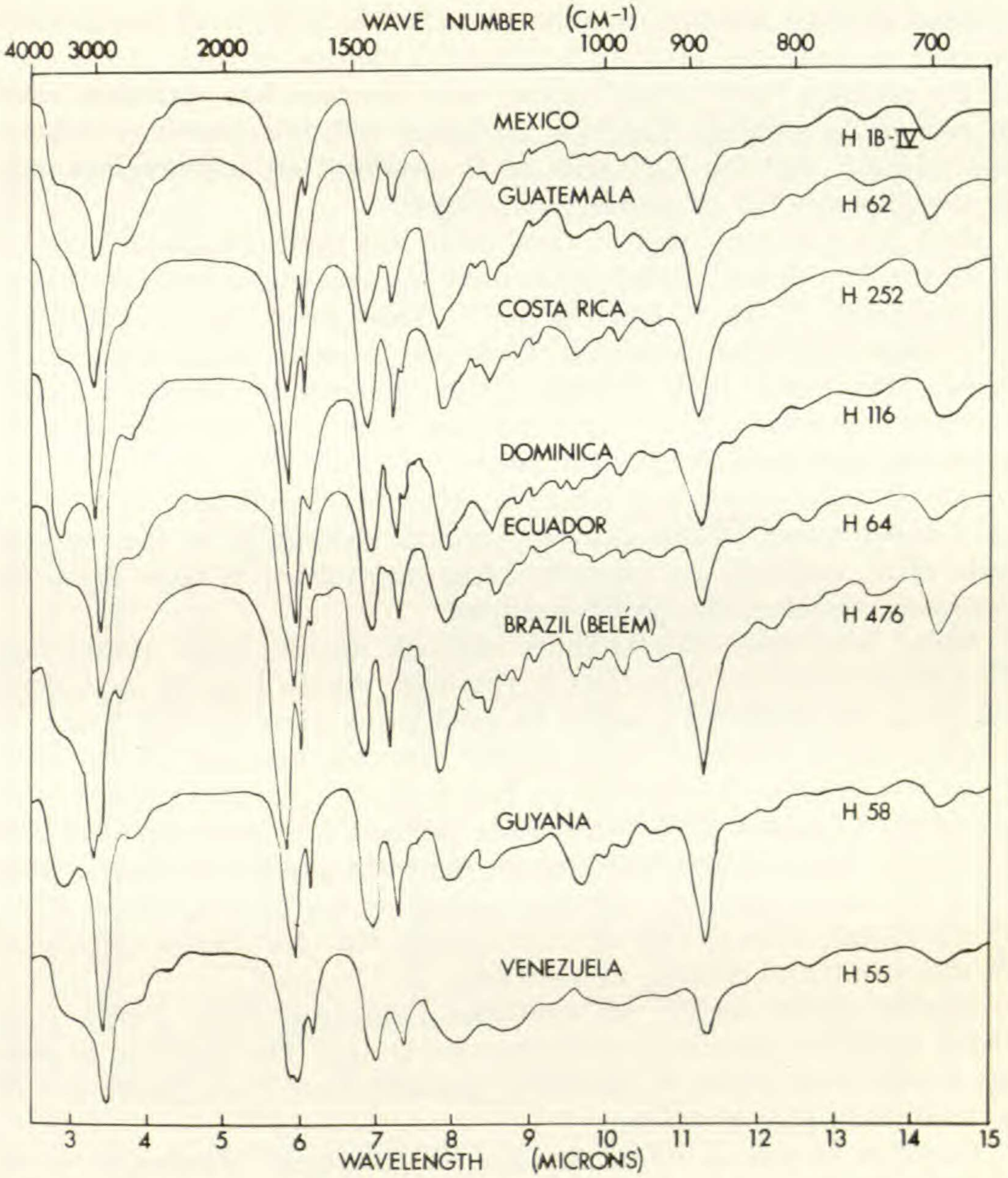

FIG. 2. Infrared spectra of resin specimens from *Hymenaea courbaril* populations in Mexico, Guatemala, Costa Rica, Dominica, Ecuador, Brazil, Guyana, and Venezuela.

has converted to relatively stable diterpene resin acids of the abietic type (Lawrence, 1959). For possible use of the oxidized resin in reflecting specific or subspecific biochemical variation, further chemical analyses are needed.

Apart from the possible influence of ecotypic variation, Beck (personal communication, 1967) indicates that the general similarity of the spectra are in accord with the expectations raised by the gross structure of copalic acid proposed by Nakano and Djerassi (1961). The strongest carbonyl absorption in all cases lies at a wave number (1700 cm.$^{-1}$) as would be expected for α, β-unsaturated carboxylic acids, but there is evidence of lesser amounts of saturated carboxylic acids in all the samples. In most of them, this evidence is limited to changes in slope at the edge of the carbonyl band toward higher wave numbers but variations exist in some of the samples. This is in agreement with the opinion of Nakano and Djerassi, that the resin acids of *H. courbaril* are mixtures not only of stereoisomers, but of double-bond isomers.

Beck likewise states that "a remarkable and quite unexpected feature of all the *H. courbaril* spectra is the weak but unmistakable absorption at approximately 700 $cm.^{-1}$ and 750 $cm.^{-1}$. This pair of bands is associated with mono-substituted benzenes. Their low intensity might lead one to suspect that these resins contain minor amounts of relatively simple aromatic compounds, but to our knowledge none have been isolated from copals by conventional chemical means." Considerable variation in intensity of these presumably aromatic absorption bands also occurred in all samples tested. These possible chemical differences in the oxidized resin of *H. courbaril* are currently being investigated in more detail by analyzing extracts of the soluble fractions.

Amber from three other localities in South America gives spectra that likewise are similar to resin from *H. courbaril.* Amber from Girón, Colombia (near Bucaramanga) occurs in goldbearing alluvium and hence its geologic age is unknown. The spectra from six samples fall into two types, one of which is presented in FIGURE 1. Six spectra of amber from Medellín, Colombia, also of unknown geologic age, were run and five are similar to the pattern indicated for the Girón amber. In both of these cases the amber spectrum was more similar to the resin spectrum of *H. courbaril* from Guiana than to other spectra run. No spectra of resin of *H. courbaril* from Colombia are available.

Another amber sample was run from Capanêma, Pará, Brazil, from strata which are considered early Miocene in age. The spectrum is similar to resin from extant *H. courbaril,* especially from Pará, Brazil, as well as from Costa Rica (FIG. 3).

Variation in spectra shown through the geographic distribution of *H. courbaril* is also reflected in the amber. The spectra of the Chiapas amber are related more closely to spectra of *Hymenaea* resin from populations in Mexico and Guatemala than to those resins from populations with a more southern distribution. Therefore, it was not surprising when the spectra of amber from Girón and Medellín, Colombia, compared closely with *H. courbaril* resin from Guiana, and that the amber from Pará, Brazil, was more comparable to the resin from Pará, Brazil, than from other areas.

PRODUCTION OF RESIN

The location of the cells and tissues in which the resin is synthesized and the anatomical mechanism for its internal collection, as well as the manner of exudation, have not been adequately investigated in *Hymenaea courbaril.* Because secretion of the resin occurs in a different manner in

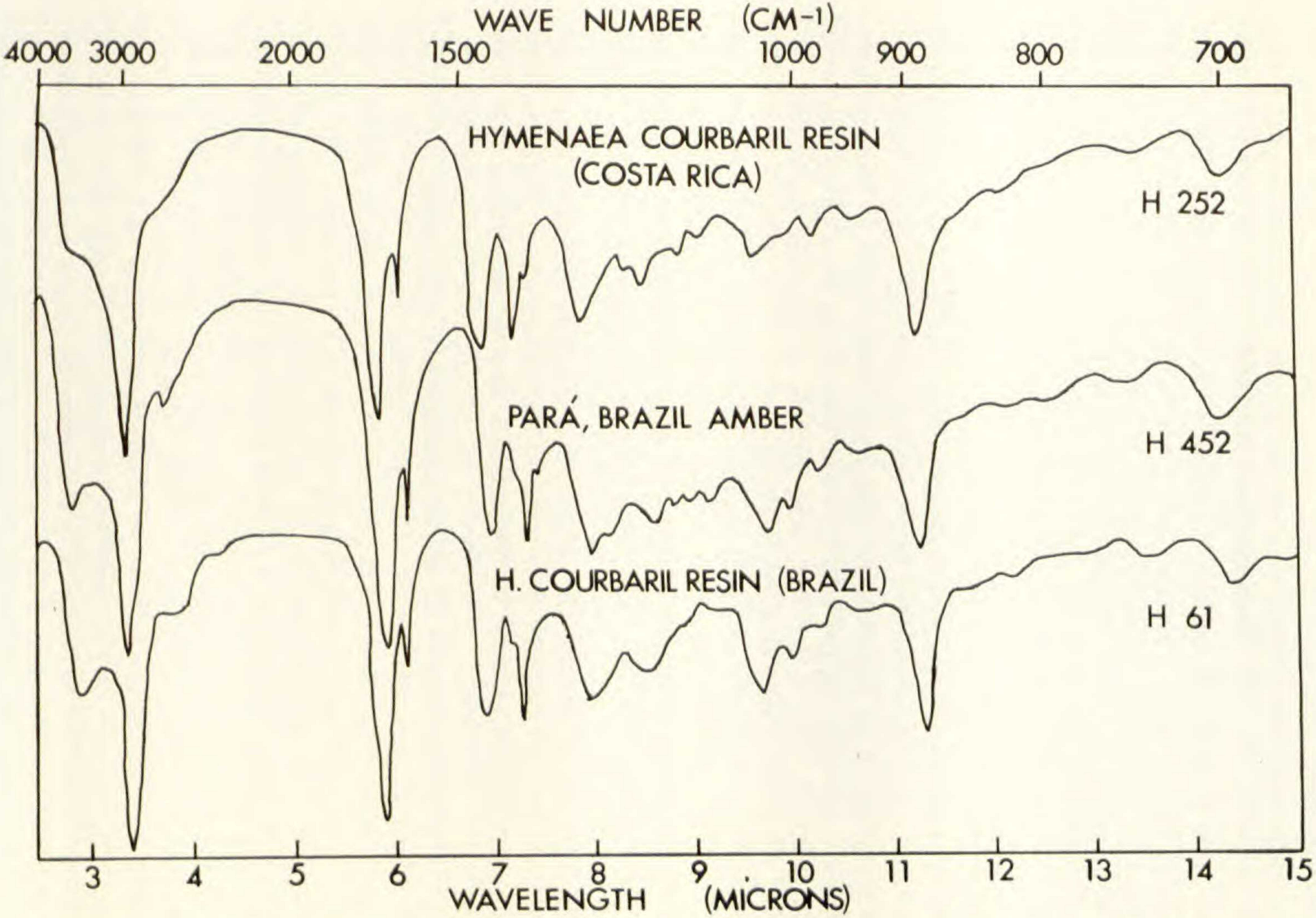

FIG. 3. Infrared spectra of Miocene amber from Pará, Brazil, and resin from extant *Hymenaea courbaril* from Pará, Brazil, and from Costa Rica.

young plants and mature trees, the secretory system is being studied from time of germination to year-old plants in the laboratory, and in older trees in the field.

MATERIALS AND METHODS

In order to study the secretory system in the young plants, seeds from Mexico, Puerto Rico, Panama, and Costa Rica were scarified, planted in sand or vermiculite and put in growth chambers (16 hour day length) at temperatures of 25° C. during the day and 21° during the night. After three months of growth in the control chambers, the plants were removed to the greenhouse. All tissue specimens of seedlings grown in either the growth chamber or greenhouse were fixed in 10 per cent aqueous acrolein (Feder, 1960) or in 3 to 6 per cent glutaraldehyde. The fixed specimens were dehydrated in a series of methoxyethanol, ethanol, n-propanol, and n-butanol, and then embedded in a monomer mixture of glycol methacrylate according to the technique of Ashley and Feder (1966). Sections were stained in aqueous 0.05 per cent toluidine blue O; in some cases they were counterstained with 1 per cent acid fuchsin or periodic acid-Schiff reagent. All sections were mounted in Permount.

Samples of branches and root suckers taken in the field in 1965 were fixed in FAA, dehydrated in an alcohol series and embedded in the previously mentioned monomer mixture of glycol methacrylate. Samples of the mature tree taken in 1966 were fixed in 10 per cent formalin in the field and post-fixed in 10 per cent acrolein upon return to the laboratory. They were taken through the dehydration schedule discussed above, except that the final changes were made in anhydrous ether. Extreme difficulty in obtaining sections of the cambial zone in *Hymenaea* had been encountered previously. Therefore a modification of the previously reported embedding mixture of glycol methacrylate was devised by Feder. The monomer mix consists of: 1) glycol methacrylate, 91.85 per cent, 2) polyethylene glycol 400, 5.0 per cent, 3) ethylene glycol dimethacrylate, 5.0 per cent and a-azodiisobutyronitrile, 0.15 per cent. The specimens then were polymerized in ¾ fl. oz. aluminum weighing pans at 60° C. overnight, followed by a 12-hour period at 100° C. It was possible to section blocks as large as 2 cm. × 1 cm., containing both wood and bark. Sections were stained with 0.05 per cent toluidine blue O and mounted in indopol polybutene H-1900, thinned to about 25 per cent in xylol in order for the sections to adhere firmly to the slide. If allowed to air dry, as with smaller sections, considerable curling and wrinkling occurred. With this technique it was possible to obtain intact sections of the cambial zone between 1 to 6 μ thick with metal knives on a Leitz rotary microtome. It also provided means of sectioning the heterogeneous cell types of phloem and xylem tissue adjacent to the cambium.

OBSERVATIONS AND RESULTS

Seedling plant: Seedlings are not commonly observed in the field.

although seeds appear to be produced abundantly. Seeds often are reported to be slow to germinate in the forest, but seedlings grow rapidly (Record & Hess, 1943). The author has observed seeds germinating in semideciduous, seasonally dry forests in both Mexico and Costa Rica just after the rainy season had begun. Seedlings were observed neither in the tropical wet forest on the Osa Peninsula of Costa Rica nor in the Amazonian forests near Belém or Manaus in Brazil. In none of these sites had trees obviously developed from seedlings. All small trees excavated were attached to roots from a large tree; thus they appear to be root suckers. Root grafts may have occurred, but this has not been substantiated. Record and Hess suggest that, because the seedlings are bushy and succulent at first, they are attractive to browsing animals. Grazing could account for lack of survival of seedlings in some sites, but seems improbable in others. Explanation for the striking lack of *H. courbaril* seedlings in the forest awaits further observation and study.

Time required for germination of seeds in the growth chambers varied considerably from the same locality as well as from different localities from Mexico, Puerto Rico, Panama, and Costa Rica. No attempt had been made to keep seeds from individual trees separate, although seeds were segregated by local populations in Mexico and Costa Rica. For example, the time of germination varied from 9 to 18 days from seeds from the same population in Guerrero, Mexico, under the same controlled conditions. Seeds from a population in Panama which germinated in 12 days in the 16 hour chamber in January, 1965, took two months in November, 1965. If germination studies per se were done, some care probably should be given to segregating seeds from individuals within a local population and to knowing the age of the pods which are collected.

At germination, the hypocotyl emerges and fleshy cotyledons are pushed above the ground. The root begins to develop rapidly, constituting approximately two-thirds of the growth for about two weeks. At this point the stem portion of the hypocotyl starts to elongate, and the epicotyl and juvenile leaves begin to develop. By 16 days the stem above the juvenile leaves has developed as well as the first pair of leaves. Although there are some differences in the length of time for development of stem and leaf, by the twenty-first day their pattern is generally developed.

Schizogenous pockets of limited size, not canals, occur in the epicotyl and in the hypocotyl to the place where root tissue begins. The pockets appear as early as three days after germination or, since the growth rate may vary, when the hypocotyl is approximately three cm. in length. In the cortex they occur one to two cells under the epidermis. They vary in number, sometimes being scattered through the cortex (FIG. 4), at other times being closely packed next to each other at least in portions of the hypocotyl or epicotyl. One to two layers of epithelial cells are common with another layer of "collapsed" cells often outside the functional layer. The pockets also occur commonly in the pith, apparently scattered at random. The pockets vary in size, but the variation in a single section may be due to cutting the pockets at different levels. Because they have an ovoid shape, a cross-sectional diameter will vary in any given section.

Petioles also present a similar morphological topography to that of the hypocotyl and epicotyl. Resin seems to be synthesized early and more of it actually appears to issue from cells in the petiole than from the hypocotyl and epicotyl. FIGURE 8 shows the general topography of the petiole. In the petiole, as well as the hypocotyl and epicotyl, the actively secreting cells are densely cytoplasmic and appear to be metabolically active (FIGS. 6 and 7). In some cells, an expansion of the cell wall is evident (FIG. 5). This expansion suggests that the resin has been secreted but not yet passed through the cell wall. Unfortunately, in these sections most of the terpenes may have been dissolved in the dehydration sequence. Also no specific stain has presently been developed which is unique for the lower terpenes, so that their presence can be substantiated. Considerably more cytological study is needed to determine the site of biosynthesis of resins in cells such as these.

Year-old plant: Periderm is initiated in the cell layer adjacent to the epidermis and forms inward into the cortex. Therefore, the secretory pockets formed early in the cortical region are preserved after the periderm has developed (FIG. 12). The extent of cortical parenchyma has decreased, however, with considerable development of phloem fibers. Pockets are not apparent either in phloem or xylem tissue, although some pockets have been maintained in the pith. Camargo (1960) noted a similar anatomical pattern for one- to two-year old stems of *H. stilbocarpa*.

The epithelial cells surrounding the pockets in year or year-and-a-half old plants do not appear to have the dense cytoplasm characteristic of the epithelial cells of younger tissue. These epithelial cells possibly are no longer synthesizing resin, but have already emptied their product into the pocket.

Resin exudes from the cortical region when the stem is cut or scraped. Wound experiments, in which pin pricks and razor slashes were made on stems of one-year old plants, were carried out. Care was necessary in any wounding experiment not to destroy completely the narrow cortical zone containing the secretory pockets. Four months following the wounding, samples of the stem were fixed, embedded, and sectioned. No evidence for an increased number of pockets was noted, nor was it possible to determine with existing techniques if additional resin synthesis was initiated.

Resin pockets have not been observed in root tissue of year-old plants.

Root suckers: As previously mentioned, all of the young trees seen in Mexico and Costa Rica appeared to have developed as root suckers. Sections of these suckers present a general anatomical pattern similar to that in the one- to two-year old stems developed from seeds. The secretory pockets, however, appear more numerous, particularly in the pith, than in the seedlings. Also considerably more resin seems to be secreted from a sucker than from a seedling stem of the same diameter. This increased production may result from the stem being attached to an extensive root system of a mature tree, where more reserve carbohydrates might be available for biosynthesis than in the seedling.

Branches: In the field, resin which had exuded in small globules along the branch was commonly observed (FIG. 15). Similar to the one-year old stem, the pockets which had their origin in the cortex have been preserved after periderm formation (FIG. 11). The resin appears superficially to be issuing through lenticels; however, in sections the pockets are not shown to have an obvious relationship to lenticels. Von Höhnel (Kisser, 1954) suggests that with increase in size of the pockets (which has been observed) the resin spontaneously bursts out of the container which is close to the periderm. As the branch enlarges, considerable cortical parenchyma is replaced by sclerenchyma, and resin is produced from cells in the cambial zone.

Globules of resin also frequently appear near the attachment of branches to the trunk. Larger masses occur associated with larger branches. These masses seem to have occurred where breaks, due to strain at the point of attachment, allow issuance of the resin which probably is produced in the cambial zone.

Fruit: Young fruits have been observed to produce such large masses of resin that they often encase the pods. Sections of fruits have not been made by the author. Ribiere (Moens, 1955) reports that fruit of *Hymenaea courbaril* contains abundant resin pockets which form in the vicinity of the epidermis in the young ovary. These pockets persist and often are engorged with resin in the wall of the older fruit.

Mature tree: The schizogenous pockets which develop in the cortex progressively disappear with the secondary development of the bark. The bark in older *H. courbaril* trees can be one to two inches thick or more. For the greater part of its thickness, the bark is highly sclerenchymatous, has relatively narrow rays, and a thin periderm. The tree can be sufficiently large and the bark so "tough" in the Amazonian region that canoes with a carrying capacity of 25 to 30 men can be made from a single tree (Record & Hess, 1943). External bark character varies in individuals. Most commonly the bark has been observed to be smooth with little rugosity (FIG. 13); sometimes a buttressing develops at the base of the tree with indication of growth stresses. In these smooth-barked trees, most of the resin seems to issue from a rupture in the bark producing vertical fissures which may be due to release of tension during rapid growth. In some cases, the smooth bark is interrupted by rugose patches (FIG. 14) and resin commonly is found in these ridges and furrows.

If a cut is made into either the trunk or root of the mature tree, resin exudes from the cambial zone. Resin is exuded in different amounts from trees of essentially the same size in the same general region, but growing in habitats with different availability of moisture. For example, resin was viscous and scantily produced from machete cuts in a tree on a dry, upland site near Villa Colón, Costa Rica. On the other hand, it was produced more abundantly and was considerably less viscous from a similar-sized tree which grew in more mesic conditions along the river near Villa Colón. Resin begins to issue soon after cutting occurs. Flowage has been observed to occur for at least six weeks, and probably longer periods could be recorded if there were opportunity for observation. Quantity of exudation depends not only on the capacity of the tree to synthesize the resin, but upon the viscosity of the resin. Also humidity conditions in the forest, which determine the rate of drying of the outer surfaces of the resin masses, are critical. In cases where the resin continues to flow for long periods despite drying conditions, sufficient pressure exists to force the mass with the oxidized surface outward. Concentric flow layers are formed within the resin mass. Often during the rainy season, the resin is beaten from the surface almost as soon as it is exuded, unless a well-oxidized crust is rapidly formed.

Although resin pockets were not noted in sections of root in the young plant, production of resin in the cambial zone of the mature root was observed. Numerous instances of small lumps of resin associated with breaks in the bark of the root were found (FIG. 16). Large masses, however, were not discovered by the author to be associated with the roots. Cuts made in excavated roots produced resin copiously and the mature root appears to have a capacity to synthesize the resin similar to that of the trunk. Questions have arisen as to the role of resin production from the roots in accounting for the large accumulations of resin in the soil around the tree. The location of resin three feet or more beneath the soil surface has been cited by Noriega (1918), Record and Hess (1943), and others as indicating that resin production underground by roots is likely. Yet it seems difficult to understand the mechanism whereby large masses of resin are produced underground, unless considerable pressure pushes the resin out into the surrounding soil. From both observation and wounding experiments no doubt exists that roots have the capacity for synthesis, and that they are highly susceptible to types of injury that would result in exudation. Adequate assessment, however, has not yet been made of the relative roles of resin production by trunk and root and subsequent accumulation of resin in the soil. Since extensive accumulations of resin occur primarily around large trees, it might be assumed that these are old trees. Thus time would have been provided for resin that had fallen from the tree to have become incorporated in the soil. In tropical areas where *Hymenaea* grows, however, the trees do not develop annual growth layers so that determination of the age of trees is difficult. Also, little is known about the rate of soil formation in these types of forest. Leaf litter is strikingly lacking and there is no basis for knowing how long it would take to incorporate lumps of resin that have fallen from the tree to any depth within the soil. In areas in Chiapas, Mexico, the resin was observed to have flowed into sand, cementing the grains into large lumps to a depth of at least six inches. On the Osa Peninsula of Costa Rica large pieces of resin had obviously fallen from long (up to 2 feet) resin stalactites hanging from the trunk and other masses incrusting the bark around fissures. Some resin lumps were incorporated in the surface of the soil above the level of the roots and hence were probably produced from the trunk.

Sections made initially of trunk and root tissue where resin was issuing did not show evidence of pockets; probably as a result of separation of the samples at the delicate cambial zone. Sections using the methods developed by Feder show the development of pockets or cavities of varying size in the cambial zone (FIGS. 9 and 10). These pockets form between the rays in a zone of undifferentiated xylem tissue. The cells in the zone where the cavities develop appear not to have become lignified as indicated by the red-violet color of the staining of the toluidine blue O. Lignified walls are blue-green in color and occur in tracheid and vessel cells just inward from the zone where the pockets form. The pockets apparently develop by cells breaking down and releasing resin into the cavity which is being enlarged, with subsequent breakdown of additional cells. The origin of these cavities would probably be considered lysigenous as compared with schizogenous separation of cells in the young plant (Esau, 1964). These pockets apparently can merge to form larger cavities, a process shown beginning in FIGURE 10. Longitudinal sections of the particular specimens examined thus far have not shown if these cavities can attain any sizable vertical extent. The particular secreting layer of cells with characteristically dense cytoplasm that occurs in schizogenous pockets of the young plant, is not evident in the lysigenous pockets. These cavities apparently develop when a sufficient break in the bark has disturbed the cambium. As yet it is not known if resin production in the mature tree is restricted to this cambial zone or if individual parenchyma cells are capable of production in the newly differentiated phloem as well as in the rays. The relatively quick exudation of the resin after cutting seems to indicate that individual cells have already synthesized the resin or that precursors are present so that the final stages of synthesis are accomplished rapidly following injury. It seems unlikely that the large quantities of resin observed can be produced from a single, relatively narrow zone of pockets along the cambium as shown from the sections presented here. More extensive cavities probably are developed or at least biosynthesis must be kept in a very active state for a relatively long period to produce the large accumulations of resin found. These conditions need further investigation before an understanding of the anatomical organization for resin production in *Hymenaea courbaril* is reached.

A pressing question raised at this point is whether or not pathological conditions are necessary for production of resin in the mature tree. As just pointed out, schizogenous resin pockets arise early as a part of the normal pattern of development in the young plant, but disruption of tissues in the cambial zone seems necessary for development of pockets in the mature plant. Even though disturbance of the cambial tissue occurs, diseased or physiologically weakened conditions are not indicated. On the contrary, the largest, most vigorous trees growing in what appear to be the most favorable environmental conditions (i.e., excellent water relations and fertile soils) are clearly those observed to be producing the most resin.

Insect damage has often been suggested to account for injury that might increase resin production. Stephen L. Wood, a specialist in the study of Central American bark beetles, reports that beetles of the Scolicidae are the most likely to produce damaging effects on a tree such as *Hymenaea* (personal communication, 1966). He, however, has not witnessed these beetles injuring *H. courbaril* in his experience in Central America. In fact, on the Osa Peninsula of Costa Rica he has observed a species of *Platypus* (a platypodid ambrosia beetle) that started tunnels it never completed, having been forced out by resin. He also noted that profuse quantities of resin were produced in large trees. In one case he states that deposits "more than an inch deep, four inches wide and a foot or two in length" were removed from an area of longitudinal furrows and ridges (Wood, personal communication, 1966). He further indicates that all tissues were healthy, with no hint of insect, fungal or other damage than forced separation of tissues from internal pressure. He offers the explanation that *H. courbaril* appears to grow slowly as a subdominant, but when an opening occurs, growth is extremely rapid until maturity is reached. During this period growth might be so rapid that the bark cannot accommodate the expansion in certain areas of stress and bark ruptures. Thus Wood's observations support those of the author's in that the large quantities of resin appear to be produced by healthy trees growing rapidly, and that insect damage apparently does not play a role in inducing pathological conditions.

The apparent individual variation in resin production in *Hymenaea courbaril* might be explained from evidence on comparative yields in certain pine populations. Resin yields have been shown to be under genetic control in *Pinus palustris* Mill., *P. caribaea* Morelet and *P. elliottii* Engelm. Snow (1949, 1954) reports that certain individuals of *P. caribaea* and *P. elliottii* yield two and one-half times as much resin as that of the average tree of the same size growing under similar conditions. No single or combined external characteristics, or environmental conditions, were discovered to set these trees apart. Squillace and Dorman (1961) and Squillace (1966), in breeding experiments on the variation and inheritance of resin yield in *P. elliottii*, have shown that this trait not only varies highly among individual trees, but is strongly inherited in comparison with most biological traits. A strain of slash pine has been developed that will yield about twice the normal amount of resin of average trees. Their results also suggest that resin yield is positively correlated with growth rate. Squillace points out that, although they selected mainly for resin yield in their experiments, the high resin producing strain also yields about 12 per cent more volume growth than normal strains. Dyer (1963) states that the quantity of resin manufactured is directly proportional to the size of the crown of slash pine.

Boudreau and Schopmeyer (1958) have noted that physical factors relating to resin flow from wounds in *Pinus elliottii* are number and size of resin ducts, pressure, and viscosity. Both resin pressure and viscosity are under strong genetic control. Duct size and number vary with stem age. Pressure and viscosity seem unaffected by stem size above 5 cm. diameter but the ratio of pressure to viscosity accounts for a substantial amount of yield variation. They also indicate that resin pressure in trees varies with environmental conditions, particularly with water relations.

Thus these studies on some pines indicate that resin yield is under genetic control, but likewise environmental conditions are important in producing favorable growth conditions that affect pressure and viscosity. These data also suggest that vigorously growing trees, rather than diseased, physiologically weakened ones, give the greatest resin yields.

DISCUSSION AND SUMMARY

Preliminary investigations of *Hymenaea courbaril* have provided evidence that at least some angiosperm resin producers living under tropical conditions do not need to be diseased or physiologically weakened by insect, fungal or other attacks to produce large quantities of resin. Resin is produced and can accumulate in sufficient quantity to account for large deposits of amber. Although these studies do not necessarily provide answers to the accumulation of the Baltic amber deposits, they do turn our attention to certain important aspects of resin production by angiosperms as well as gymnosperms. In order to assess the capacity of members of various species of *Hymenaea* to produce resin, as well as to account for differences in chemical composition of the resin, further systematic analysis of the group is needed. Particularly, more ecologic and genetic data in terms of the development of physiological races would be valuable. Studies of the unoxidized resin (i.e., the volatile terpene fractions) from populations of *H. courbaril* might show differences in composition related to ecotypic differentiation. Striking similarity of infrared spectra of oxidized resin from specimens throughout the wide range of distribution of *H. courbaril* may result from chemical stability of the diterpene copalic acid constituent. This copalic acid also may provide the basis for relating the present-day *H. courbaril* resin to amber of Oligo-Miocene age from Mexico, Miocene from Brazil, and unknown age from two localities in Colombia.

In the anatomical adaptation for resin production in *Hymenaea courbaril*, schizogenous pockets form in cortical and medullary tissue of the epicotyl and stem (but not the root) portion of the hypocotyl soon after germination. These pockets persist until bark formation finally obliterates them. In the older plant, lysigenously developed cavities appear in the cambial zone of the trunk or root. It seems unlikely that the narrow zone of pockets in the cambial zone can entirely account for the large quantities of resin that are produced, even allowing considerable time for production. Although not observed yet, more extensive cavities may be formed by enlargement of the existing ones. Whether or not parenchyma cells in the living phloem or in the xylem rays also synthesize resins is still questionable. There also is question as to whether continual stress of some sort is needed to keep the enzymes active for continued biosynthesis when lysigenous breakdown is involved.

Although not demonstrated as yet, it seems likely that resin yield in *Hymenaea courbaril* is under strong genetic control, as has been shown for several species of pine. Local populations of *H. courbaril* in particular geographic regions have been noted for outstanding resin yields by commercial resin collectors. This fact, however, does not sort out the genetic factors from the environmental ones. The largest, most vigorously growing trees have been observed to produce the greatest amounts of resin, which possibly may be due to excess carbohydrate available for synthesis of a secondary product. Therefore, superimposed upon genetic capacity, all environmental factors that result in greater net photosynthesis, and hence possible higher growth rates, may increase synthesis. Partial explanation for the large number of different kinds of trees producing resin, which occur in tropical regions, as well as particularly high resin yields, may be provided by the favorable growth conditions throughout the year. Experimental work is needed to substantiate these possibilities. Likewise, vigorous growth activities of these tropical trees may help account for means of exudation which augment those resulting from injuries due to storms, insect and fungal infestations, etc. This leads then to the *raison d'être* for biosynthesis of resin and its possible evolutionary significance. The metabolic role of these terpenoids which constitute resins still is obscure; the prevailing idea is that they simply represent ways of disposing of excess acetate. Thus the primary significance of these terpenoids may be ecologic, in providing protective adaptation against such damage as is inflicted by insects and fungi. Abnormal flows of resin are known to be stimulated by wounds and by the presence of fungal disease. Also terpenoids can act as excellent fungicides and insecticides and their presence in a tropical environment, where both fungi and insects are abundant, could provide a selective advantage. With more studies of the chemistry of these terpenoids making up resins, their biogenesis, and their discharging processes, however, a metabolic role may possibly be discovered that would augment the ecologic, protective role.

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EXPLANATION OF PLATES

PLATE I

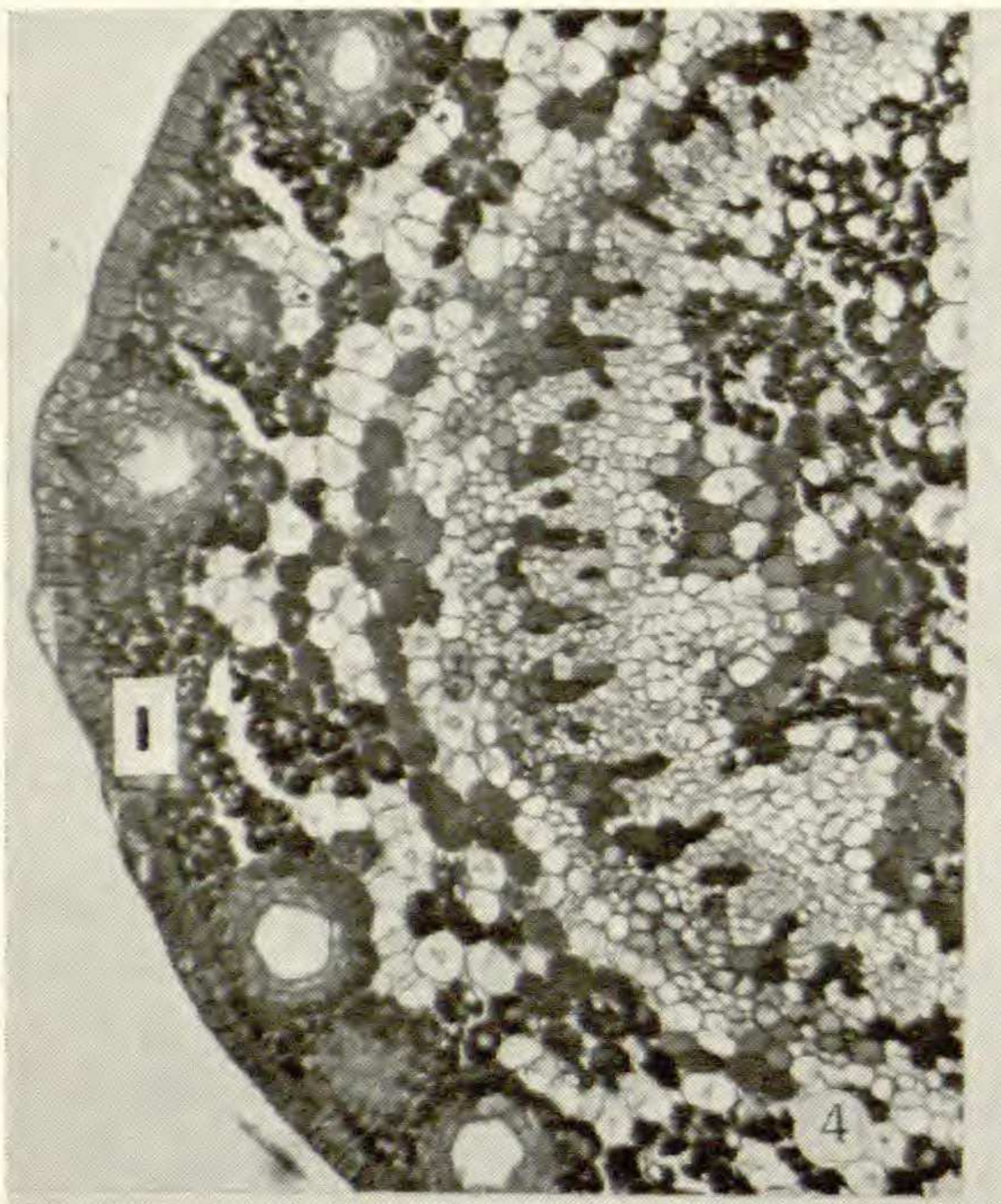
FIGS. 4–8. Transverse sections of *Hymenaea courbaril* (Mexico). 4, topography of epicotyl, 21-day old plant, showing location of resin pockets in cortex near epidermis; 5, resin pocket from epicotyl (FIG. 4) near epidermis, with distention of cell walls in secreting cells; 6, resin pocket in pith of petiole, (FIG. 8) showing densely cytoplasmic secreting cells; 7, resin pocket from cortex of petiole; 8, topography of petiole showing extensive development of resin pockets in cortex and pith. Line scale on all figures is 50μ.

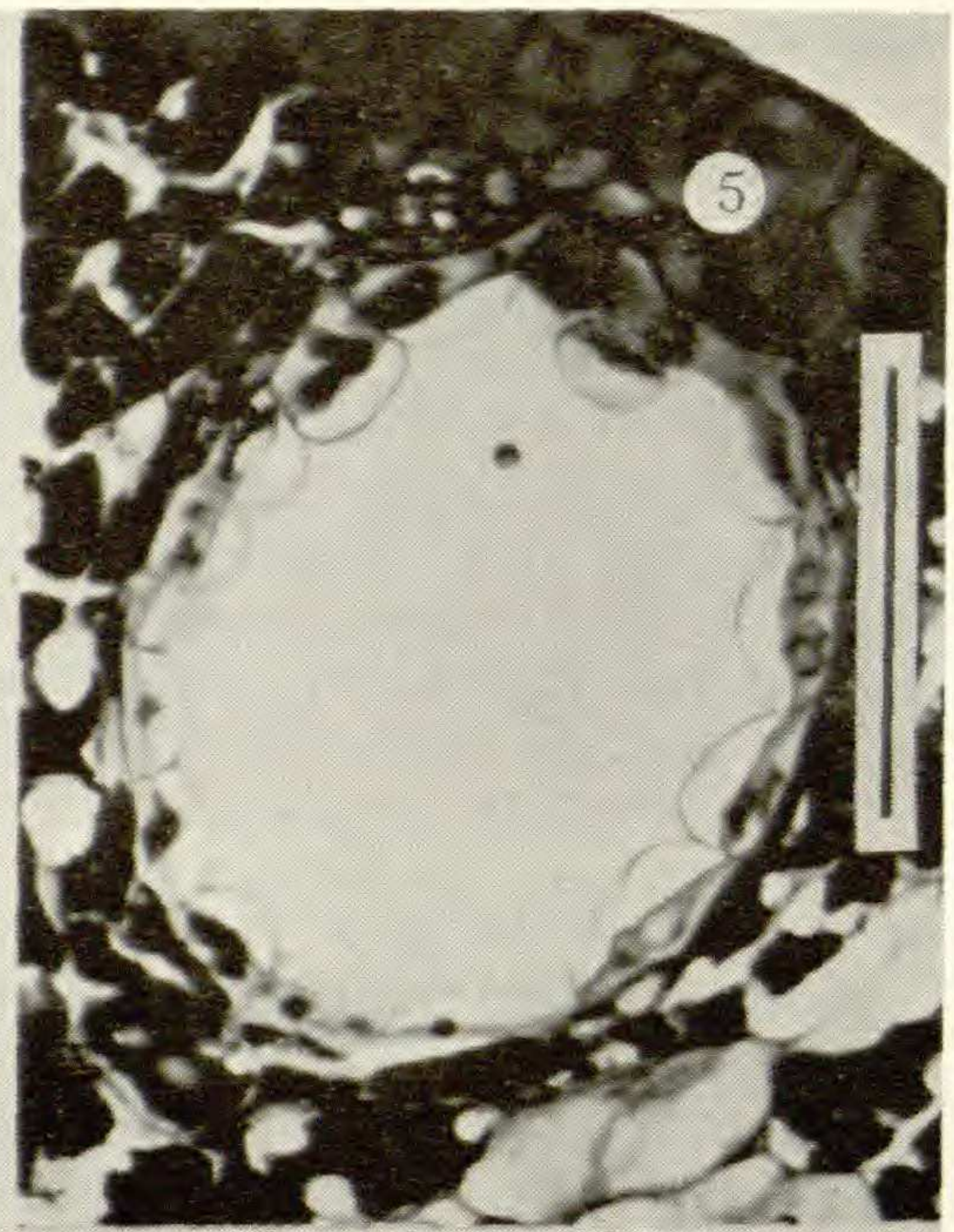
PLATE II

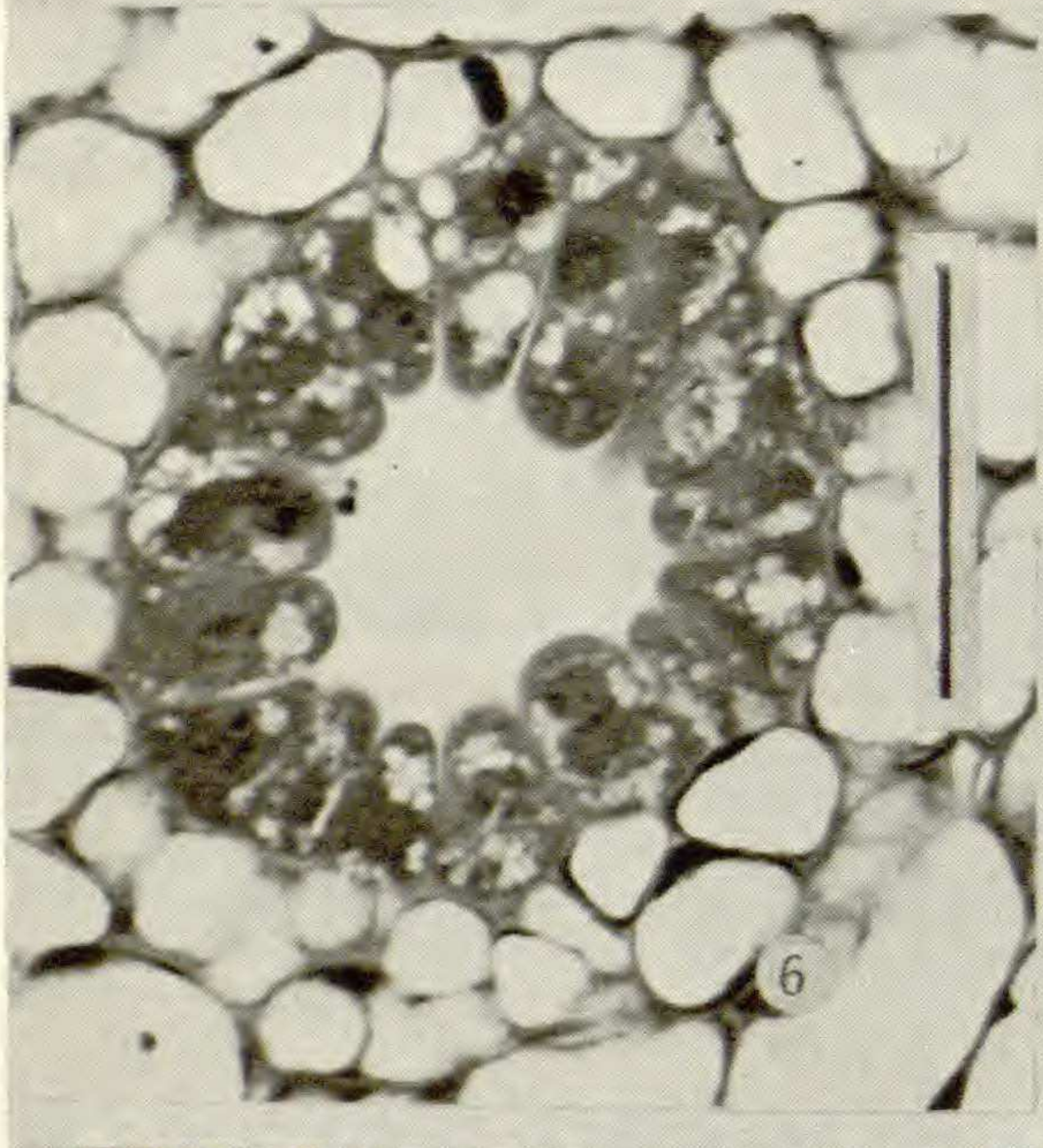
FIGS. 9–12. Transverse section of *Hymenaea courbaril*. 9, pockets developed in cambial zone of trunk of mature tree, Belém, Brazil; 10, pockets similar to FIG. 9 but showing coalescence to form cavities; 11, branch, Manaus, Brazil, showing preservation of pockets in the cortex amid extensive development of sclerenchyma; 12, one-year old stem, Mexico, showing preservation of pockets after the periderm starts to develop. Line scale on all figures is 50μ.

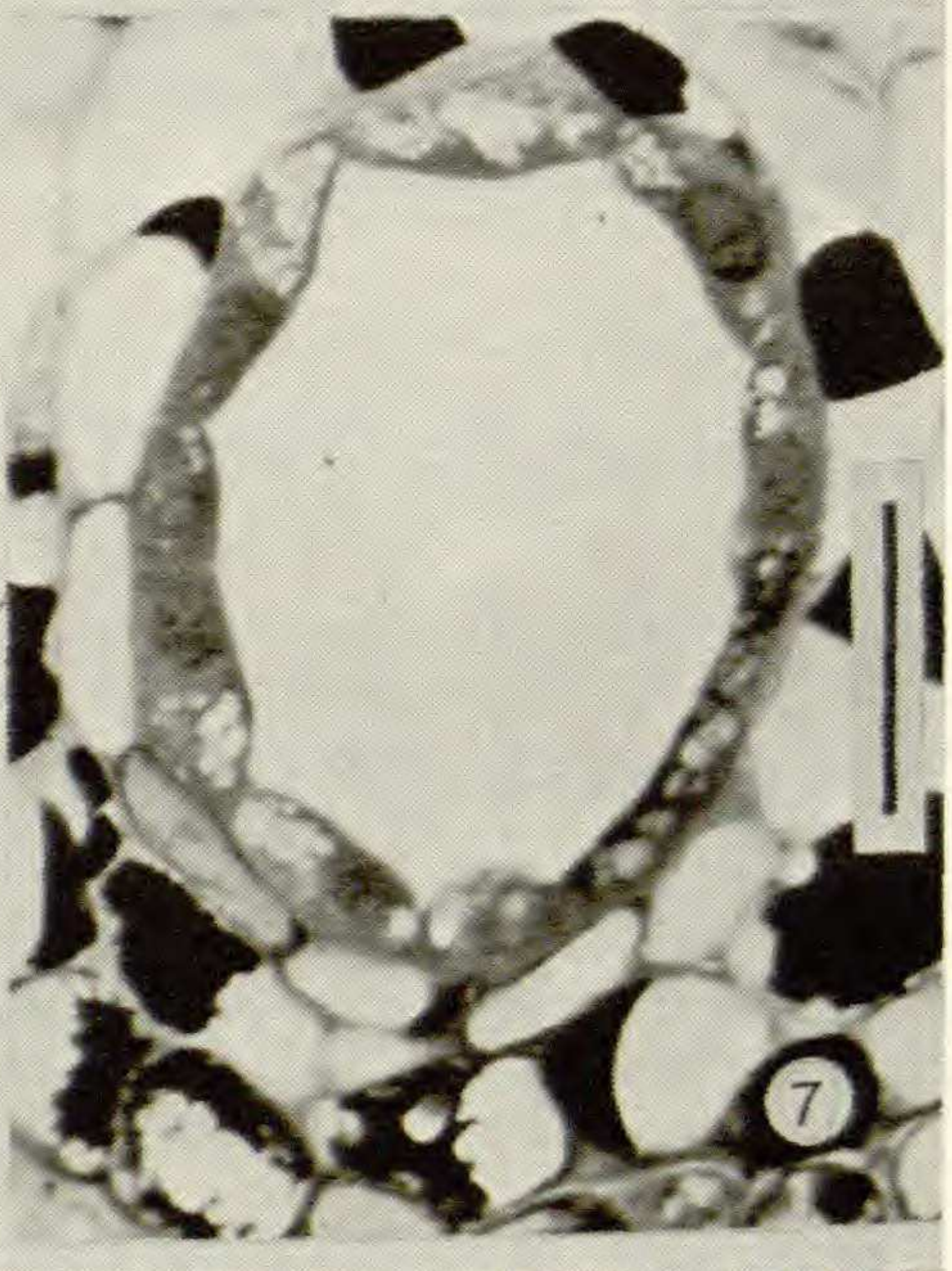
PLATE III

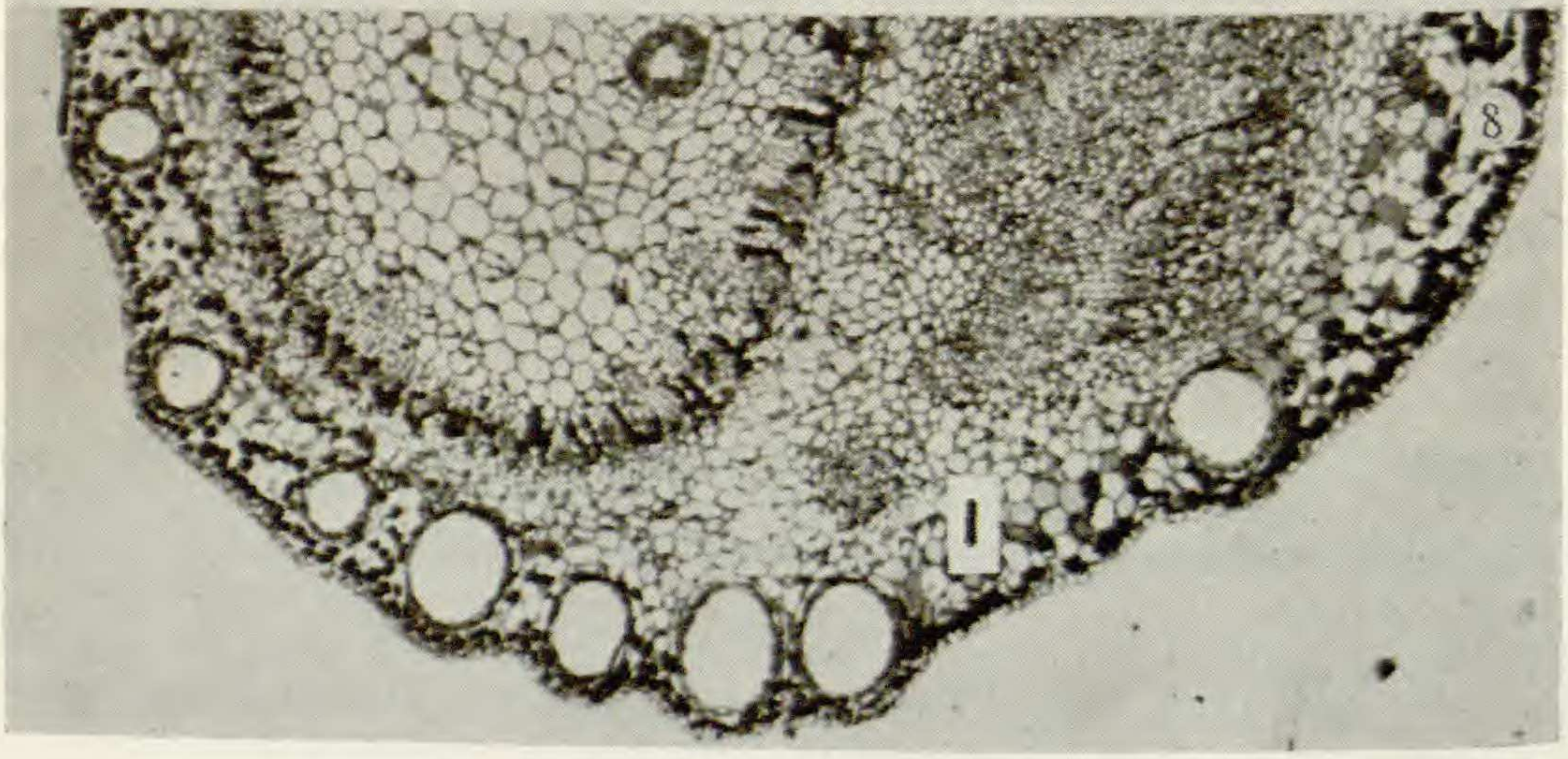
FIGS. 13–16. Field conditions in which *Hymenaea courbaril* is found. 13, typical mature tree with smooth bark, tropical dry forest, Guanacaste, Costa Rica; 14, tree with rugose patches in bark, subdeciduous forest, Guerrero, Mexico; 15, branch showing exuded balls of resin, Guerrero, Mexico; 16, injured root with associated small masses of resin, Guerrero, Mexico.



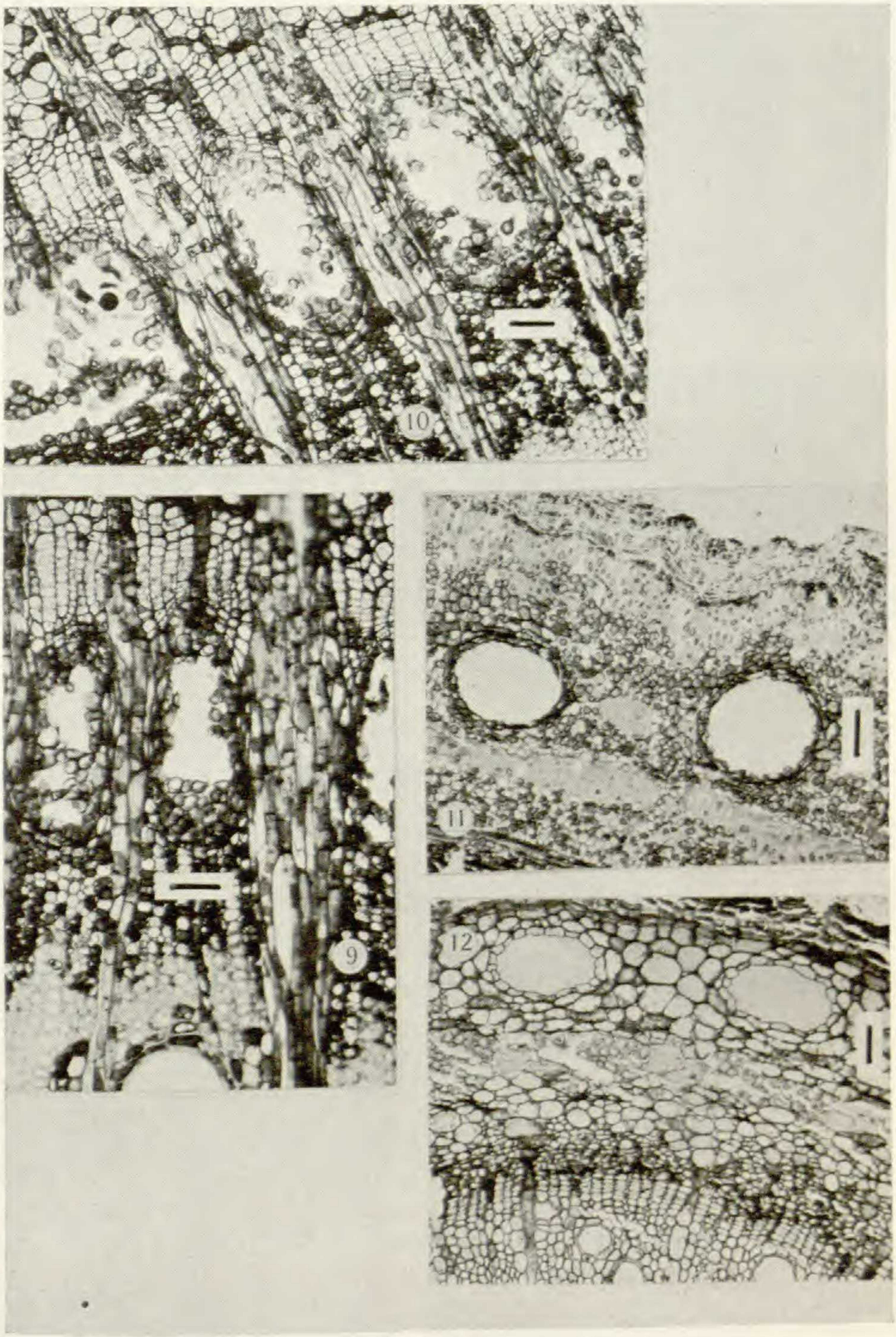








LANGENHEIM, HYMENAEA COURBARIL



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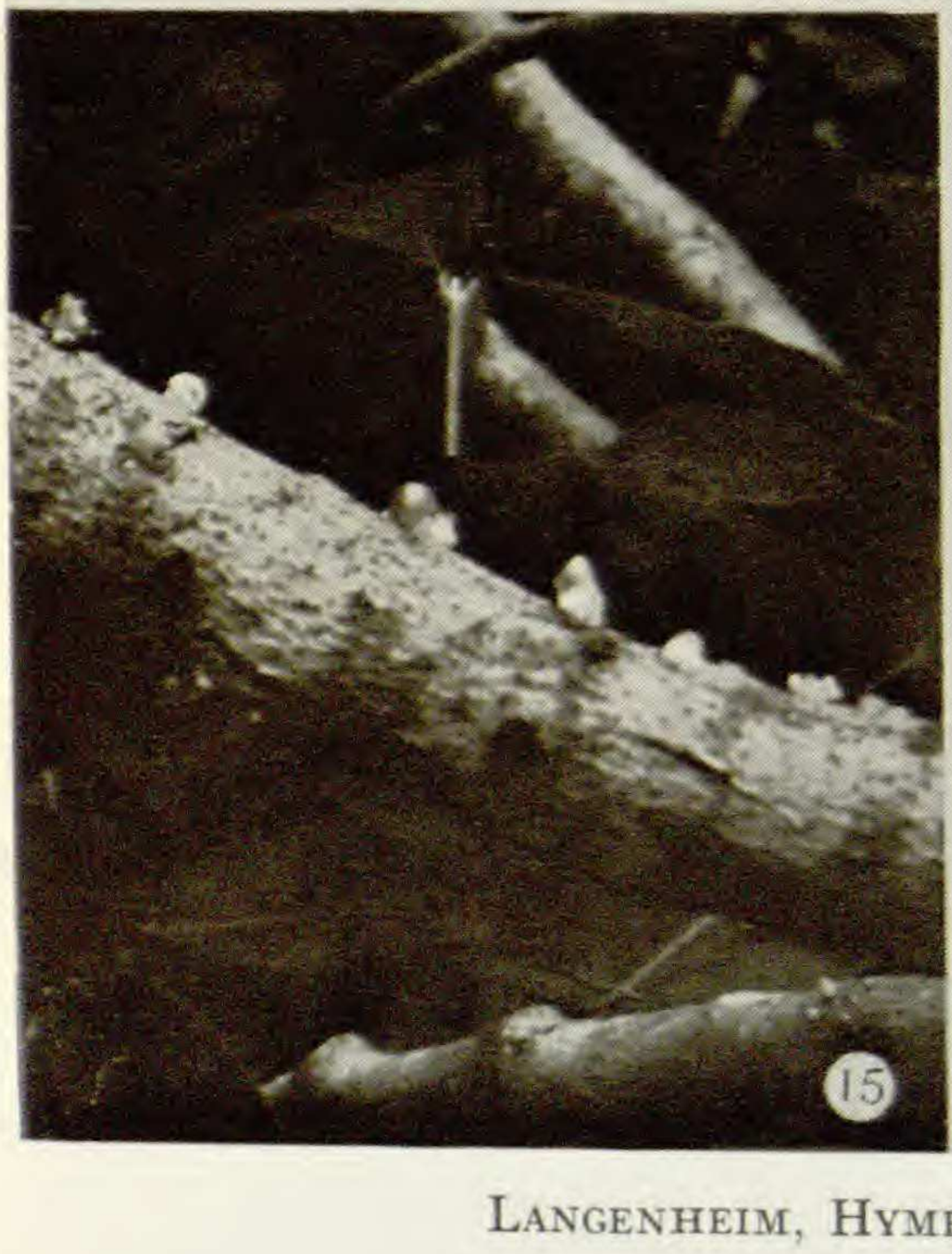

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